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Burrow Structure and Foraging Costs in the Fossorial Rodent, *Thomomys bottae*

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Summary. A model for calculating the energy cost of burrowing by fossorial rodents is presented and used to examine the energetics of foraging by burrowing. The pocket gopher *Thomomys bottae* (Rodentia: Geomyidae) digs burrows for access to food. Feeding tunnels of *Thomomys* are broken into segments by laterals to the surface that are used to dispose of excavated soil. Energy cost of burrowing depends on both soil type and on burrow structure, defined by the length of burrow segments, angle of ascent of laterals, depth of feeding tunnels, and burrow diameter. In a desert scrub habitat, *Thomomys* adjust burrow segment length to minimize cost of burrowing. Observed segment lengths (mean = 1.33 m) closely approximate the minimum-cost segment length of 1.22 m. Minimizing energy expended per meter of tunnel constructed maximizes efficiency of foraging by burrowing in the desert scrub. Burrow diameter and cost of burrowing increase with body size, while benefits do not, so foraging by burrowing becomes less enconomical as body size increases. Maximum possible body size of fossorial mammals depends on habitat productivity and energy cost of burrowing in local soils.

Introduction

Natural selection should favor behavior that optimizes benefits of foraging relative to costs. Much of optimal foraging theory and tests thereof deal with behavior patterns that maximize benefits, usually food biomass or energy obtained. The most extensive development of this theory deals with optimal diet breadth (Emlen 1966; MacArthur and Pianka 1966; Schoener 1971), and several quantitative studies directly test predictions of this part of optimal foraging theory (see Pyke et al. 1977 for review). Relatively little attention has been devoted to analysis of costs of foraging, or the way cost varies with different patterns of foraging, because the means of estimating costs have not been readily available to field biologists. This gap can only be filled by integrating physiological measurements of animal energetics with field observations of foraging behavior.

The most successful example of such integration has been study of the economics of foraging behavior of nectar feeding birds (Gill and Wolf 1975a, b; Wolf 1975; Wolf et al. 1975; Carpenter and MacMillen 1976) and bees (Heinrich 1979 and references therein). Similar analyses for other groups have lagged because of the absence of physiological data for estimating the costs or the difficulty in accurately recording foraging behavior and estimating benefits.

Fossorial rodents, which feed only on plant material that they can obtain without leaving their burrow system, provide a convenient system for analysis of the costs of foraging. Though they are difficult to observe directly, their burrow systems provide a durable and reliable record of past foraging activity. Energy cost of burrowing can be measured in the laboratory (Vleck 1979), and used to estimate energy expenditure in the field. In this study I examine the energy cost of foraging by burrowing in the fossorial rodent *Thomomys bottae* and analyze the way cost varies with burrow structure. In one particular habitat, *Thomomys* maximize foraging efficiency by adjusting burrow structure to minimize the energy expended per meter of burrow.

The Animal

Thomomys bottae is a pocket gopher of the family Geomyidae (Rodentia). Like all geomyids, *Thomomys* are highly fossorial and spend most of their lives within burrows. Their natural history has been discussed by Howard and Childs (1959) and Miller (1957). *Thomomys* are morphologically specialized for burrowing (Hollinger 1916; Hill 1937), and construct extensive burrow systems that they use not only for shelter but for access to food. They feed on plant material encountered during burrowing or harvested from the surface within a body length of burrow opening (Grinnell 1923; Aldous 1951; Howard and Childs 1959). *Thomomys* may move across the surface when forced out of their burrows (Ingles 1949), when dispersing from natal burrows (Hansen and Miller 1959; Vaughn 1963) or when seeking mates (Howard and childs 1959), but rarely or never leave the burrow system to forage on the surface away from a burrow opening.

Cost of Burrowing: Measurements and Models

Burrow Structure

Burrow structure, that is, the physical dimensions and geometry of the burrow system, can have a large impact on the energy cost of burrowing. Burrow systems of pocket gophers consists of superficial feeding tunnels and a set of deeper chambers used for food storage and nesting. Because construction of the deeper chambers is not a foraging activity, I will not discuss them further.

Feeding tunnels usually constitute 80% or more of the total burrow system (Miller 1957). They run parallel to the surface of the ground and are punctuated by two types of passages to the surface – popholes and laterals. Both types are usually kept plugged with soil when not actually in use. Popholes are short tunnels, extending a few cm to one side or the other of the main tunnel and often ending in a vertical rise of 5 to 10 cm to the surface. They are used for access to the surface

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to harvest surface vegetation. Laterals are usually much longer than popholes. Surface feeding occurs at the ends of laterals as well as at popholes, but laterals are also used to push excavated soil out of the burrow system onto the surface and are marked by mounds of soil.

Figure 1 illustrates those structural features that affect cost of burrowing and are under proximate control of an individual pocket gopher. These include burrow depth, segment length (distance between laterals) and angle of ascent of laterals. Minimum burrow radius is determined by the body size of the burrower, and is subject both to evolutionary (genetic) control and to environmental control by factors such as food availability or food quality.

Costs of Shearing and Pushing Soil

Energy use in burrowing is partitioned between shearing soil loose and pushing it out of the burrow. I have previously measured costs of shearing and pushing soil in *Thomomys bottae* (Vleck 1979). Briefly, energy used for shearing is proportional to the mass of soil sheared loose and energy used for pushing is proportional to both the mass of soil removed and the distance it is pushed. The total cost for digging a level burrow when the excavated soil is dumped at the entrance is given by:

$$E_{\text{seg}}=K_s(C)\,(S)+K_p(C)\,(S)\,(^1/_2 S) \tag{1}$$

where E_{seg}=energy cost of digging a burrow of length S, K_s= energy required to shear 1 kg of soil loose, K_p=energy required to push 1 kg of soil 1 m, and C=mass of soil removed per m of tunnel. That is, $C=\pi r^2 \rho$ where r is burrow radius and ρ is soil bulk density. The total mass of soil removed is $(C)(S)$, and $(^1/_2\, S)$ is the mean distance this soil is pushed. The proportionality constant K_s and K_p are calculated by fitting Eq. (1) to values of energy expended (measured as oxygen consumption in an open circuit system) as a function of burrow length. Costs of burrowing varies with soil type and with the efficiency of the burrower. Mean values of K_s for *T. bottae* range from about 330 $\text{J}\cdot\text{kg}^{-1}$ in fine sand to 2,970 $\text{J}\cdot\text{kg}^{-1}$ in clay, and the values of K_p range from about 580 $\text{J}\cdot(\text{kg}\cdot\text{m})^{-1}$ in sand to 2,830 $\text{J}\cdot(\text{kg}\cdot\text{m})^{-1}$ in clay (Vleck 1979).

Calculating cost of burrowing

Equation (1) describes the energy cost of constructing a level burrow of length S when the soil excavated is disposed of at the starting point of the burrow segment. It must be extended to calculate cost of constructing a typical feeding tunnel.

A feeding tunnel can be treated as a series of segments each associated with a lateral to the surface (Fig. 1). Soil excavated in digging a segment is pushed out of a lateral and disposed of as a mound on the surface. At the end of each segment, a new lateral is excavated and the preceding one is packed with soil. The cost of digging a feeding tunnel is therefore not just the cost of digging a tunnel segment of the appropriate length, but includes the cost of digging the associated laterals and also the work done against gravity in raising soil to the surface.

To model this situation, I assume that all of the soil removed from a given tunnel segment is pushed out onto the surface through the preceding lateral and all of the soil excavated from a new lateral is used to refill the preceding one. The results are insensitive to minor violations of these assumptions. I also assume energy expended doing work against gravity is 20% efficient (Cavagna et al. 1964). Gravitational work is a negligible fraction of the total and efficiency could vary widely without significantly affecting the results.

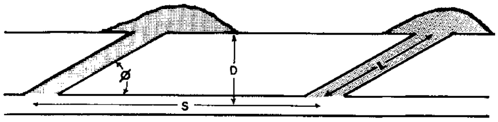

Fig. 1. Diagrammatic sketch of a section of *Thomomys* feeding tunnel. The two laterals are marked by mounds of soil at their ends on the surface. *D* is depth of main tunnel, *S* the segment length between laterals or between mounds, *L* the lateral length, and ϕ is the angle of ascent of the lateral

The total mass of soil removed from a typical segment of feeding tunnel including the associated lateral is $(C)(S+L)$, where L is lateral length in m. The soil from the burrow segment proper, a mass of $(C)(S)$, is pushed a mean distance of $(^1/_2\, S+L)$ to the surface. It is raised a distance D against the acceleration of gravity in the process. The soil from the lateral, a mass of $(C)(L)$ is pushed a distance $(S+L)$, and is raised a mean distance of $(^1/_2\, D)$. The energy cost of digging a segment of feeding tunnel including the associated lateral is then:

$$E_{\text{seg}}=C(S+L)\,K_s+C(S)\,(^1/_2\, S+L)\,K_p+C(L)(S+L)\,K_p \\ +5\,(C\cdot S\cdot g\cdot D)+5\,(C\cdot L\cdot g\cdot {}^1/_2\, D) \tag{2}$$

where g is the acceleration due to gravity. The energy cost per meter of feeding tunnel is:

$$E=\frac{E_{\text{seg}}}{S}. \tag{3}$$

The cost-of-burrowing model given by Eqs. (2) and (3) allows calculation of the energy expended in digging a burrow of a given structure, and evaluation of the way cost varies as the parameters defining burrow structure vary. It allows comparison of actual cost of burrowing in a particular system with the range of possible costs, and determination of whether pocket gophers adjust burrow structure to control foraging costs. Such quantitative evaluation requires measurement of burrow structure in the field in a soil type for which costs of shearing soil loose (K_s) and pushing soil (K_p) are known.

Field Observations

Study Area

I examined burrow systems of *Thomomys* in East Deception Canyon on the south edge of the Little San Bernardino Mountains of Riverside County, California. Pocket gopher burrow systems were located on sandy bajadas or alluvial fans dissected by shallow dry watercourses. The study area was selected on the basis of soil conditions, habitat productivity, and pocket gopher distribution.

Soil in the study area was a deep, gravelly sand with no perceptible differences in soil structure to a depth of two meters. It was not cohesive, so soil structure and density were easily duplicated in the laboratory for burrowing experiments. Soil bulk density (ρ) at a depth of 25 cm averaged 1,620 $\text{kg}\cdot\text{m}^{-3}$ (SE=20). For *T. bottae*, K_s in this soil averaged 335 $\text{J}\cdot\text{kg}^{-1}$ (S.E.=74) and K_p averaged 452 $\text{J}\,(\text{kg}\cdot\text{m})^{-1}$ (S.E.=107) (Vleck 1979).

Vegetation in the area was a low desert scrub, dominated by the perennial shrubs *Larrea divaricata, Encelia farinosa,* and *Ambrosia dumosa.* The shrubs occur in discrete patches, each representing one or more bushes. Patches were spaced 2 to 4 m apart and usually separated by bare ground. Annuals were present only for a few weeks following winter or spring rains, and were most abundant around the bases of patches of bushes. Between patches annuals were more widely spaced and often entirely absent. The primary productivity and thus food availability to a herbivore in a desert scrub community is among the lowest reported for terrestrial communities (Whittaker 1970). Such a community provides a system in which energy balance is likely to be marginal, so that adaptations improving foraging economics are strongly favored.

Burrow Systems

Pocket gophers (*Thomomys bottae perpallidus*) were present in low density throughout the study area. Burrow systems were usually isolated from each other, sometimes by more than 100 m. This minimized the amount of digging necessary to distinguish burrow systems of individuals; in most cases systems could be mapped from the mounds of soil pushed out on the surface. All of the feeding tunnels of four systems were excavated and mapped, and other systems were mapped from surface indications. Length of feeding tunnels in systems inhabited by adult *Thomomys* ranged from 30 to 75 m.

Feeding tunnels comprise most of the burrow system and are easily recognized. They were relatively linear and often maintained a very constant heading; changes in direction of more than 15 or 20° usually occurred only at intervals of 5 to 30 m, or when a tunnel encountered a barrier such as a rock outcrop. Most feeding tunnels were between 15 and 35 cm below the surface. Mean depth was 27 cm (S.E. = 0.7; $n=95$ observations on four burrow systems). Tunnel radii ranged from 2.5 to 3.7 cm; both extremes occurred in the same burrow system. Mean tunnel radius was 2.95 cm (S.E. = 0.02; $n=165$ observations on four burrow systems).

The length of laterals (L in m) was related to the depth of the main feeding tunnel (D in m) by the equation:

$$L = 2.95\,\mathrm{D} - 0.24 \qquad (n=25;\ r^2=0.62). \tag{4}$$

The coefficient of D is significantly different from zero ($P<0.01$). This corresponds to an angle of ascent of about 30° from the horizontal for laterals which ascend to the surface from a feeding tunnel that lies 27 cm below the surface.

Distance between laterals, corresponding to segment length S in Fig. (1), averaged 137 cm (S.E. = 13; $n=29$). Mean distance between the mounds marking the ends of adjacent laterals for all of the burrow systems examined was 133 cm (S.E. = 3; $n=269$). The distance between mounds is not significantly different from segment length measured by excavating burrow systems ($P<0.05$), so I combine both measurements in subsequent analysis.

Is Cost Minimized?

Do *Thomomys* adjust burrow structure to control foraging costs? The field data and the cost-of-burrowing model provide an answer. From Eqs. (2) and (3) the energy cost per meter of feeding tunnel can vary with segment length, lateral length and burrow depth.

Segment Length

When segment lengths are short the energy cost per meter burrowed is high, even though soil is never pushed far for disposal, because the pocket gopher must dig many laterals to the surface. As segment length increases, the number of laterals per meter of tunnel decreases, reducing the total amount of soil that must be removed and the energy expended in shearing soil loose. However, soil must be pushed farther and the cost of pushing increases. Energy cost per meter is minimal at some intermediate segment length. Cost of burrowing, calculated from Eq. (3), is plotted as a function of segment length for burrows of three different depths in Fig. 2. Soil density and burrow radius were assumed to equal mean values observed in the field. Lateral length was adjusted for burrow depth using Eq. (4), and K_s and K_p were those for soil from the study area.

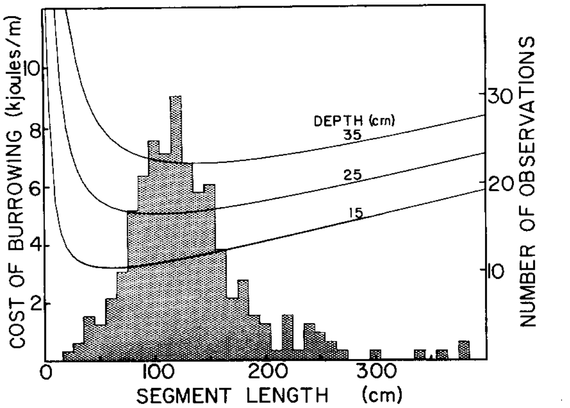

Fig. 2. Smooth curves describe the energy cost of burrowing as a function of segment length for feeding tunnels at three different depths. Superimposed is a histogram showing the distribution of segment lengths observed in the study area

Observed segment lengths, as indicated by distance between adjacent mounds, lie near the lengths predicted by the model to minimize energy cost of burrowing (Fig. 2). The segment length corresponding to the minimum energy cost per meter burrowed, calculated by differentiating Eq. (3) is:

$$S_{\text{min cost}} = \sqrt{\frac{2K_s \cdot L + 2\,K_p \cdot L^2 + 5\,g \cdot D \cdot L}{K_p}}. \tag{5}$$

Segment length that minimizes cost for a feeding tunnel 27 cm deep, the mean observed depth, is 1.22 m. The observed mean segment length is 1.33 m, with a modal length between 1.2 and 1.3 m. The cost of burrowing is within 10% of the minimum cost at segment lengths between 0.6 and 2.4 m; 90% of the observed segment lengths lie within this interval. The correspondence between the geometry of predicted minimum cost and that observed in the field suggests that pocket gophers in this habitat minimize the energy expended per meter burrowed or equivalently, maximize the distance burrowed for a given energy expenditure.

Lateral Length

Lateral length has substantial impact on the cost of burrowing. If *T. bottae* constructed shorter, vertical laterals instead of longer, gently sloping laterals, cost of burrowing could be reduced by about 30% for a burrow 27 cm deep, assuming that the animals were equally efficient in pushing soil out of a vertical lateral (Fig. 3). Laterals are not vertical because this assumption does not hold in sandy soil.

Thomomys in cohesive soils often dig nearly vertical laterals and have little difficulty pushing lumps of excavated soil out or plugging the lateral afterward (unpublished data). However, in cohesionless sands like those in the study area, pocket gophers' efficiency in pushing soil obviously declines as slope increases. At steep angles of ascent, much of a load of sand may fall back down the tunnel, increasing the number of trips necessary to push a given amount out. Laboratory observations indicate

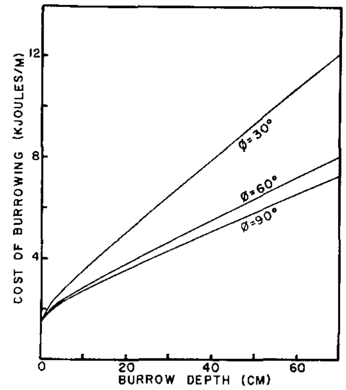

Fig. 3. Effect of angle of ascent of laterals and burrow depth on energy cost of burrowing. Smooth curves are calculated from Eqs. (2), (3), and (4) for laterals ascending to the surface at the indicated angles

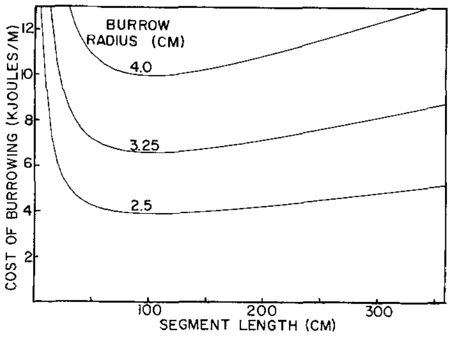

Fig. 4. Effects of burrow radius and segment length on the energy cost of burrowing

that *T. bottae* may also have difficulty in plugging the surface openings of vertical tunnels in cohesionless soils. The slope of laterals is probably dictated by soil characteristics and the differential efficiency of pushing soil with changes in slope. Laterals that ascend at shallow angles may be the most efficient solution in sandy soil.

Burrow Depth

Cost of burrowing increases with burrow depth (Fig. 2) primarily due to the correlation between depth and lateral length [Eq. (4)]. This is particularly true in cohesionless soils where the angle of ascent is small (Fig. 3). Work performed against gravity in pushing soil out of a burrow is proportional to burrow depth, but the energy cost of working against gravity is small relative to the cost of shearing and pushing soil. From Eq. (2), gravitational work is only about one percent of the total required for a 122 cm burrow segment at a depth of 27 cm.

Minimum burrow depth may be controlled primarily by factors other than the short-term energy cost of burrowing. Shallow tunnels in sandy soil readily cave in as the soil dries out. Shallow tunnels dry out more quickly, are subject to greater temperature fluctuations, and are easily destroyed by any large animals stepping on the surface above them. Because feeding tunnels are re-used, shallow tunnels that require frequent repair may be uneconomical investments.

Why Minimize Costs?

Thomomys bottae in the study are select burrow segment lengths that minimize cost per meter burrowed. How does this affect the economics of foraging?

Food resources for a herbivorous rodent in the creosote bush scrub habitat are limited in abundance and heterogeneously distributed. Most of the primary productivity of plant material occurs in and under the patches of perennial shrubs (Halvorsen and Patten 1975). Once a gopher encounters such a patch, it is exploited extensively; there are always popholes and other signs of feeding activity. The cost of such exploitation is low compared to the cost of burrowing between clumps. Therefore, it is reasonable to assume that the potential benefits of foraging are proportional to the number of clumps encountered.

There is no evidence that *Thomomys bottae* can detect shrub clumps from a distance in this habitat. Their vision is poor under any circumstance and useless underground. Burrows may pass within 50 cm or less of a clump of bushes without ever entering the clump. These observations, together with the generally constant heading of feeding tunnels, suggest that encounters with clumps are stochastic events, dependent on the density, and size of the clumps and the length of the feeding tunnel. If probability of encountering a clump is proportional to total burrow length, and if benefits of foraging are proportional to the number of clumps encountered, then minimizing cost per meter burrowed maximizes foraging efficiency, defined as the ratio of benefits gained to costs incurred in digging a feeding tunnel. *Thomomys* could increase foraging efficiency by detecting the next nearest clump and burrowing directly to it. However, since shrub clumps are approximately evenly spaced (mean nearest neighbor distance is 3.45 m [$n=41$; S.E.$=0.18$]) the total number of clumps encountered would still be proportional to burrow length. Minimizing burrow cost would still maximize foraging efficiency.

Body Size, Cost of Burrowing, and Habitat Productivity

Burrow Radius

Energy cost of burrowing is directly proportional to the mass of soil removed and thus to the cross-sectional area of the burrow (Fig. 4). For *T. bottae,* radius of freshly-excavated burrows is related to body mass as $r=0.91\ M^{0.27}$, where r is radius in cm and M is body mass in g (Vleck 1979). Because cross-sectional area is proportional to the square of radius, cost of burrowing is roughly proportional to the square root of body mass. *T. bottae* from my study area averaged 65.2 g; a pocket gopher weighing twice as much would expend 45% more energy in burrowing a given distance, and a gopher four times as large would use more than twice as much energy for burrowing. In addition, energy expenditure for maintenance and other activities would also increase with body size.

Maximum Body Size

Energy harvested, or benefits of foraging by burrowing, cannot increase indefinitely with burrow cross-sectional area because plant productivity is not uniformly distributed through the soil column. Because benefits ultimately depend on burrow length and costs increase with both length and cross-sectional area, foraging economics place an upper limit on body size of fossorial animals (Fig. 5). The maximum permissable size will depend on habitat productivity and cost of burrowing in local soils, but we can make the qualitative predictions that (1) maximum body size of fossorial mammals will increase with habitat productivity, and (2) at constant productivity, maximum body size will increase as soils grade from indurate to friable where cost-of-

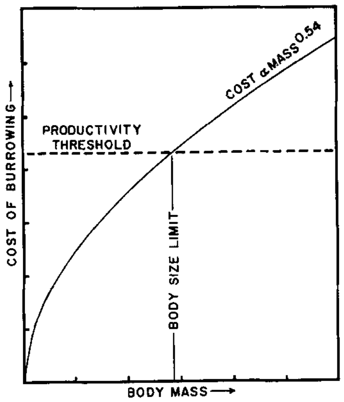

Fig. 5. Energy cost of burrowing increases with body mass of the burrower. Maximum possible body size for fossorial mammals is the size at which benefits of foraging by burrowing are equal to costs. Level of this threshold is set by habitat productivity, which determines benefits, and local soil type, which determines minimum costs

burrowing is lower. Schoener (1969), Hainsworth and Wolf (1972), and Wolf et al. (1975) have proposed similar hypothesis relating body size, foraging costs, and energy availability based on data from lizards and nectar-feeding birds.

Average adult body size increases with habitat productivity in the pocket gophers *Geomys bursarius* and *G. personatus* (Kennerly 1959), and *Thomomys quadratus* and *T. bottae* (Davis 1938). On a larger scale, plant primary productivity tends to increase latitudinally from polar to equatorial regions (Ricklefs 1979). Body size of geomyids follows a similar latitudinal trend. The largest member of the family, of the genus *Orthogeomys*, reach 800–900 g and are restricted to southern Mexico and tropical central America (Walker 1975), while *Thomomys talpoides*, the species whose range extends furthest north, is among the smallest members of the family with adults ranging from 78 to 130 g (Burt and Grossenheider 1976). Where ranges of two species of pocket gophers meet, the larger species is found in the more favorable habitat, and the smaller species is restricted to the less productive area or less friable soil (Miller 1964). Available data appear to confirm predicted trends in body size.

McNab (1979) proposed thermoregulatory stress may be an important factor controlling body size and distribution of fossorial mammals. In some cases, thermal stress and foraging economics may select for similar characteristics (Vleck 1979). Either low productivity or high soil temperatures might be important factors in excluding large fossorial mammals from hot deserts. However, in other cases, predictions based on thermal stress are not congruent with those based on energetics. For example, McNab's (1979) arguments suggest maximum body size of fossorial mammals should decrease as soil temperature increases, and therefore predict a latitudinal trend in body size opposite to that observed in geomyids (see above). Foraging economics and habitat productivity appear to provide a better explanation of body size limits and pocket gopher distribution than does thermoregulatory stress.

Energy, Natural Selection, and the Fossorial Niche

The fossorial niche offers shelter from the surface environment, an escape from surface predators, and access to underground food resources. These advantages are gained at the expense of a high energy cost for foraging by burrowing. Burrowing from one point to another can be 360–3,400 times as expensive as moving the same distance across the surface (Vleck 1979). Adaptations that affect energy balance and cost of foraging are subject to relatively intense selection in fossorial animals. Therefore energetics provides a conceptual framework that can organize a variety of observations on fossorial mammals.

The cost-of-burrowing model I have discussed here provides order to observations of burrow structure and body size, and is a quantitative tool for further investigations of the energetics of fossorial mammals. The Ctenomyidae and Octodontidae of South American, the Spalacidae of Eurasia, and the Bathyergidae and Rhizomyidae of Africa all include representatives that resemble pocket gophers in appearance and natural history (Ellerman 1956). Constraints imposed by the fossorial niche, which have led to the evolution of considerable convergence in the physiology and morphology of these fossorial rodents (Eloff 1951; Ellerman 1956; McNab 1966), mean that the conclusions developed here should be applicable to these distantly related but convergent groups. In turn, the convergent groups provide possible independent tests of the cost-of-burrowing model and the hypotheses derived from it.

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